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A review of the distribution and ecology of the elusive Brown Hairstreak butterfly *Thecla betulae* (Lepidoptera, Lycaenidae) in the Iberian Peninsula

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Abstract. The Brown Hairstreak (*Thecla betulae* L.) is one of the least observed butterflies of the Palaearctic region, even though its distribution spans from Portugal in the west, to Russia and Korea in the far east. Adults are arboreal and seldom descend to ground level. As a result, this species is mostly monitored via the detection of eggs on the food plant during wintertime. In the Iberian Peninsula, this species was largely unknown until very recently, but a recent burst of regional studies in Spain has begun bridging this gap. However, their focused nature and a still incomplete knowledge on *T. betulae* in Portugal promoted the need for an integrative study at the Iberian scale.

Here, we carried out a full literature review on the distribution, ecology and behaviour of *T. betulae* in Portugal and Spain. Complemented with field work in Portugal, we revealed an almost continuous distribution in the northern third of Iberia, whilst populations further south are mostly mountain-bound. In order to help with future discovery of new populations, we built a species-distribution model relating its occurrence with bioclimatic variables. This model accurately explains the current known occupation of the territory and highlights other areas where the species may potentially be found. Finally, we found evidence of a broadening of the species' niche through the local use of an hitherto unknown food plant. This study sets a new knowledge baseline for future works and conservation of *T. betulae* through southern Europe.

Introduction

The Brown Hairstreak, *Thecla betulae* (Linnaeus, 1758) is a widespread trans-Palaearctic species known from Portugal in the west (Maravalhas et al. 2004), to the Pacific coasts of Russia and Korea in the far east (Weidenhoffer and Bozano 2007). This temperate woodland species has its southernmost areas of occurrence in the Iberian Peninsula and northern Turkey (Kudrna et al. 2011).

Before 1999, when the species was recorded for the first time in Portugal (Maravalhas 2003), the species' Iberian distribution was considered to be traditionally limited to the temperate Euro-Siberian northern third of Spain (García-Barros et al. 2004). However, a plethora of more recent studies have greatly enhanced its known regional distribution area, not only bridging this distribution-gap, but also expanding its known biology and ecology at the local scale, such as most recent Spanish references, to the macro-scale of more integrative studies across Europe.

Throughout its wide range, *T. betulae* occurs in temperate woodlands, hedgerows, forest edges and extensively managed agricultural land, whenever its food plant resource is available. *T. betulae* is moderately polyphagous (Fiedler 1991) and caterpillars feed on a variety of rosaceous shrubs and trees in the genus *Prunus*, especially on Blackthorn (*Prunus spinosa*). Other species of *Prunus* are used, but also *Crataegus monogyna* and *Chaenomeles japonica* (Dantchenko et al. 1995; Tolman and Lewington 1997; Tshikolovets 2011; Mortera 2015; Leraut 2016). All of these plant species are closely related within the subfamily Amygdaloideae of the Rosaceae family and are secondary components of many temperate vegetation communities. The sister species *Thecla betulina* Staudinger, 1887, which is restricted to the far East of Asia in the Amur, Korea and NE China, is also dependent of allied plants but is apparently restricted to *Malus manchurica* and *Pyrus* species (Shirôzu 1962; Dantchenko et al. 1995).

T. betulae is an univoltine species with adults on the wing from July to October in one extended generation. Overwintering happens in the egg stage, which are most often laid at the base of lateral shoots of the food plant, and positioned between half a metre and two metres above ground (Fartmann and Timmermann 2006; Williams 2007; Merckx and Berwaerts 2010). In early spring, right after the mass flowering of the host plant, young caterpillars emerge synchronously with the first leaves and feed on their underside, until pupation by May or June, which is either accomplished at ground level in the leaf litter or on nearby branches.

Adults (butterflies) are particularly difficult to locate as they are seldom seen on flowers. Instead, they mostly occur at canopy level, feeding on tree sap, aphid secretions and dew (Emmet and Heath 1990; Jubany and Stefanescu 2007). Only during early morning or under adverse weather condition do they descend to lower levels. A common statement in most studies about the species is that even experienced lepidopterists have seen the imago relatively few times, even compared to other arboreal and related species such as *Favonius quercus* (Linnaeus, 1758).

Therefore, by far the preferred method to study this species is to search for the bright white overwintering eggs on the dark-coloured bark of blackthorn and related food plants from autumn to early spring (Fartmann and Timmermann 2006; Merckx and Berwaerts 2010). Detection of eggs is relatively easy because their colour contrasts well with bark and because the host plants are deciduous, shedding their leaves during winter. This method has in fact yielded the overwhelming majority of Iberian and European records of the species and its ease probably also explains why *T. betulae* appears to be one of the most studied butterflies in the western Palaearctic.

In Portugal, the species' late addition to the national species list is undoubtedly a reflection of this elusive life style. Only in 2011 was a live adult observed, a considerable time after the first detection of the species in 1999. This first record was a deceased adult, and was observed by two of the authors of this study. At the time, this observation came from a highly unexpected location (Maravalhas 2003; Maravalhas et al. 2004) as Serra da Lousã was a long way from the nearest known localities in Galicia back in 1999.

Since then, more observations on the species have accumulated in both Portugal and Spain. In the former, the published precise occurrence of *T. betulae* in Portugal came from only six localities (Maravalhas et al. 2004) and the species was generally known to be present in another five UTM 10 km quadrats (Vicente Arranz et al. 2013b) in three widely separated geographic areas: 1) the western Central Mountain System in Serra da Lousã (one locality in one quadrat); 2) the Central Mountain System near the international border around Serra da Malcata (five quadrats); 3) the south-western extremity of the Galician Massif near Serra de Montesinho (five localities in three quadrats). However, a proper assessment on the species' ecological needs and conservation in a meaningful biogeographic unit requires a modern overview of all evidence pertaining to the occurrence of this species in both countries. Also, because of the generally regional approach this species has received in Spain, scattered over many journals, books and reports, we took the opportunity to carry out a *Thecla betulae* literature review on the distribution and ecology (behaviour, food plant use and other relevant biological data) in the whole of the Iberian Peninsula, aiming to set the baseline for further studies and conservation measures in the whole of Iberia.

Materials and methods

Literature review

Garcia-Barros et al. (2004) in the Atlas of Iberian butterflies provide the first comprehensive summary of butterfly records known in Iberia up to the date of its publication (2004). For *Thecla betulae*, the atlas compiles 122 landscape-scale quadrats (10 × 10 km) as the Iberian distribution of the species. However, the extensive gaps in between some of the confirmed presence areas were a sign there was still much to discover on the Iberian distribution of the species. As is generally often the case after the publication of atlases, this work promoted the search for the species in many new places, as shown by the various publications since 2004, in the (mostly) Spanish scientific literature. Therefore, we have considered only the period of 2002–2021, since the publication of the Atlas, in our literature revision.

New records and fieldwork

The general presence of potential food plants throughout at least the northern part of Portugal together with suitable climatic and habitat conditions, were indicative that the butterfly could be more widespread than suggested in previous works (Maravalhas et al. 2004; Vicente Arranz et al. 2013b). Likely areas to support *T. betulae* were opportunistically surveyed from 2004–2021, during the summer for adults (May-September) or later for eggs (August-June). We complemented these surveys with findings reported to us on social media (e.g. Facebook). In this species, eggs, larvae and adults are of straightforward visual morphological identification, and no confusion with other species is expected. The number of eggs on each host plant was then counted, and the putative food plant species was recorded, alongside location data such as coordinates and altitude.

Species distribution mapping and niche modelling

Formally published Iberian information and newly acquired fieldwork records were complemented with distribution data available from the GBIF database (GBIF.org 2021), taking advantage of the recent development of citizen-science projects all over the world and the online availability of museum collections. All these records allowed us to build an up-to-date distribution map of the

species in the Iberian Peninsula. As a means of standardisation with previous works and for viewing purposes, we converted all point coordinate and UTM area data to 10 × 10 km UTM quadrats, implementing the final dataset in QGIS v.3.10.2 (QGIS.org 2021).

In order to help increase the focus of future search campaigns, we performed species distribution modelling using maximum entropy analysis implemented in MAXENT v.3.4.1 (Phillips et al. 2006). Our Iberian dataset totals 442 single *T. betulae* occurence points, which we contrasted against 19 current bioclimatic variables from the WORLDCLIM database (www.worldclim.org; Fick and Hijmans 2017), clipped to the Iberian peninsula. For the estimation of the current potential distribution of the species, we ran the program at default settings for 1,000 bootstrap replicates using 75% of species localities as training data, and the remaining 25% to test the model. The result was a heat-map in shades of green, from light green (little predicted presence) to dark green (maximum predicted presence) for the whole of Iberia.

Results

Iberian literature

A detailed revision of the literature dealing with *T. betulae* in Iberia yielded nine papers focused exclusively on this species in the region: Viader (1994), Stefanescu (1997), Stefanescu (2000), Vicente Arranz et al. (2013a), Vicente Arranz et al. (2013b), Vicente Arranz and Arjona (2014), Antón and Beltzunegi (2015), Mortera (2015) and Salvadores Ramos and Salvadores Ramos (2018). Many others do address important ecological and/ or distribution data, albeit not exclusively about *T. betulae* (e.g. Gómez de Aizpúrua 1991; García-Barros et al. 2004; Maravalhas et al. 2004; Sanjurjo Franch 2007; Monasterio León et al. 2014a, 2015; Vila et al. 2018; Salvadores Ramos and Salvadores Ramos 2020). One study (Dinca et al. 2015), delves into the genetics of the species: the authors found only two COI haplotypes in Iberia, among the six scored throughout Europe (from Portugal to Russia), in a shallow and non-geographically-structured differentiation pattern.

The majority of studies combine field-detection of eggs with food plant usage in order to only produce distribution maps. A few studies describe the early stages (Gómez de Aizpúrua 1991; Stefanescu 1997; Muñoz Sariot 2011), whilst two behavioural ecology studies focus on larval interactions with ants (Stefanescu 2000) and adult selection of master trees as interaction grounds for this canopy dweller butterfly (Jubany and Stefanescu 2007).

Regarding Portugal, we found only one article dedicated to the species (Maravalhas et al. 2004), although another one (Vicente Arranz et al. 2013b) provided some observations which are unfortunately published with poor resolution to allow for checking precise locations or deeper studies other than coarse mapping. Post 2002 regional Iberian distribution works on *T. betulae* have been summarized in Table 1.

New Portuguese records

In the period 2003–2021, the authors and collaborators carried-out fieldwork in Portugal, with a positive detection for *T. betulae* in 19 new sites. This presence was confirmed over the years in several of these new localities as well as in previously known ones. All currently known Portuguese records of *T. betulae* are shown in detail in Table 2.

Portuguese records cluster in three to four different areas. The largest majority of occurrence sites are located along the Portuguese part of the Central Iberian Mountain System (which continues

Table 1. Literature review concerning *T. betulae* in Iberian provinces. For each province, the most relevant sources of information are mentioned as well as the number of known occupied UTM 10 × 10 km quadrats (* known before this study).

Country	Province	Relevant literature	Occupied UTM
Spain	Álava	Monasterio León et al. 2015 Iturribarria 2018	17
	Asturias	Mortera 2015	61
	Ávila	Vicente Arranz and Parra-Arjona 2010 Vicente Arranz et al. 2013b	8
	Barcelona	Viader 1994 Stefanescu 1997 García-Barros et al. 2004 Dinca et al. 2015 Anton 2018 Vila et al. 2018	25
	Bizkaya	Monasterio León et al. 2015 Iturribarria 2018	4
	Burgos	García-Barros et al. 2004 Vicente Arranz et al. 2013b Monasterio León et al. 2015 iNaturalist.org 2021	24
	Cáceres	Vicente Arranz et al. 2013a Vicente Arranz et al. 2013b	6
	Cantabria	García-Barros et al. 2004 Monasterio León et al. 2015	11
	Galicia	Fernández Vidal 2011 Pino Pérez and Castro González 2013 Fernández Vidal 2017 Salvadores Ramos and Salvadores Ramos 2018	62
	Girona	García-Barros et al. 2004 Dinca et al. 2015 Anton 2018 Vila et al. 2018	28
	Guipuzcoa	Monasterio León et al. 2015	6
	Huesca	Del Pino and Grustán 1994 García-Barros et al. 2004 Murria Beltrán 2009 Abós Castel 2013 Castilla and Cezón 2018	24
	León	Sanjurjo Franch 2007 Manceñido González and Gonzalez Estebañez 2013	27
	Lleida	García-Barros et al. 2004 Vila et al. 2018	26
	Madrid	Vicente Arranz et al. 2013b	1
	Navarra	Antón and Beltzunegi 2015	55
	Palencia	Dinca et al. 2015	4
	La Rioja	Latasa 1999 Monasterio León et al. 2014b	31
	Salamanca	Vicente Arranz et al. 2013b	22
	Soria	García-Barros et al. 2004 Vicente Arranz et al. 2013b	7
	Zamora	Vicente Arranz and Parra Arjona 2014	9
	Zaragoza	-	2
Portugal	Bragança	Maravalhas et al. 2004	4*
	Coimbra	Maravalhas et al. 2004 iNaturalist 2021	1*
	Guarda	Vicente Arranz et al. 2013b	5*

Table 2. Verified Portuguese records of *T. betulae* until 2021. Both published and new records are presented. Abbreviations: AG: Alfredo Gomes; ALS: Albano Soares; AS: Ambra Sedlmayer; AT: Álvaro Trindade; EM: Eduardo Marabuto; EMv: Ernestino Maravalhas; FR: Fernando Romão; JAF: José Agostinho Fernandes; MC: Martin Corley; PL: Paulo Lemos; PP: Pedro Pires; SL: Sandra Lopes; TM: Tatiana Moreira; TMx: Thomas Merckx. Stage key: e - egg; l - larva; p - pupa; a - adult; x - 1 to 5; xx - 5 to 10; xxx - over 10.

	Locality	County	MGRS 1 km	Altitude (m)	Date	Counts/ stage	Foodplant	Recorder	Source
1	Cerdeira, Lousã	Coimbra	29TNE6838	710	20-VIII-1999	x a	*P. domestica*	FR, PP	Maravalhas et al. 2004
					6-III-2002	xxx e			"
					22-XII-2007	xxx e			this study
					02-IV-2008	x e			this study
					22-XI-2009	x e			this study
					01-XII-2009	x e			this study
2	Cabeço Guerras, Montesinho	Bragança	29TPG8039	840	21-II-2002	x e	*P. spinosa*	AT, AS, FR	Maravalhas et al. 2004
3	Cova da Lua, Montesinho	Bragança	29TPG8139	810	III-2002	x e	*P. spinosa*	EMv	Maravalhas et al. 2004
4	Qta Tranginha	Bragança	29TPG8731	600	III-2002	x e	*P. spinosa*	EMv	Maravalhas et al. 2004
5	EN308, Montesinho	Bragança	29TPG9332	600	III-2002	x e	*P. spinosa*	EMv	Maravalhas et al. 2004
6	Montesinho	Bragança	29TPG8139	810	III-2003	x e	*P. spinosa*	EMv	Maravalhas et al. 2004
7	Gondesende, Montesinho	Bragança	29TPG7635		III-2003	x e	*P. spinosa*	EMv	Maravalhas et al. 2004
8	Beça, Boticas	Vila Real	29TPG0815	790	20-IX-2003	x e	*P. domestica*	EM, PP	this study
9	Pena, Góis	Coimbra	29TNE7340	660	28-XII-2007	xx e	*P. domestica*	FR, PP	this study
					1-XI-2009	x e			
10	Folques, Arganil	Coimbra	29TNE8352	250	1-XI-2009	x e	*P. domestica*	PP	this study
11	Souto Concelho, Manteigas	Guarda	29TPE2671	800	3-XI-2009	x e	*P. spinosa*	FR	this study
12	Trinta	Guarda	29TPE3785 29TPE3885	725	15-XI-2009	x e	*P. insititia*	PP	this study
					28-VIII-2011	x e		EM, FR, TM	
					21-XI-2013	xx e		FR, PP	
					13-II-2014	xxx e		FR	
					21-VIII-2014			FR	
13	Podre, Castro Laboreiro	Viana do Castelo	29TNG6850	800	8-IX-2011	x a	*P. domestica*	TMx	this study
					17-IX-2011	xxx e		TMx	
					9-XI-2012	x e		TMx, EM, MC	
14	Ponte da Ranca, Vinhais	Bragança	29TPG6630	400	16-V-2013	x e	*P. insititia*	EM, FR, MC, PP, TM	this study
15	Aveção do Cabo - Campeã	Vila Real	29TNF9372	780	17-VIII-2014	x a	*P. domestica*	JAF	this study
					24-VIII-2014	x a + e			
					11-I-2015	xx e			
					14-I-2015	x e			
					28-I-2015	x e			
					31-I-2015	x e			
					15-III-2015	x e			
					16-VI-2015	x e			
					28-VI-2015	x e			
					20-IX-2015	x e			
					25-X-2015	xx e			
					24-I-2016	xx e			
					6-IV-2016	xx e			
					17-V-2017	x e			
					29-VI-2017	x e			
					7-XI-2017	x e			
					16-XI-2017	x e			
					20-II-2018	x e			

	Locality	County	MGRS 1 km	Altitude (m)	Date	Counts/ stage	Foodplant	Recorder	Source
16	Arganil (South)	Coimbra	29TNE8051	210	1-VII-2014 28-IX-2014 26-VI-2015 1-VII-2015 1-VIII-2015 3-VIII-2015 6-VIII-2015 11-VIII-2015 5-IX-2015 29-II-2016 3-III-2016 11-VI-2016 12-VI-2016 16-VI-2016 11-VII-2016 24-V-2017 2-VIII-2017 9-IX-2017	x a x a x a x a x a x a + e x a x a xxx e x l x l x a x a + l x a x p x a x a x a	*P. spinosa* *P. domestica* *P. spinosa* *P. spinosa* *P. insititia* *P. spinosa*	PL	this study
17	Selada das Eiras	Coimbra	29TNE8748	795	2-V-2015 17-VI-2015 25-VI-2015 6-VII-2016 15-X-2017	x l x a x a x a x e	*P. spinosa* *P. spinosa*	PL	this study
18	Alagoa (Arganil)	Coimbra	29TNE8054	160	26-V-2015	x l	*P. spinosa*	PL	this study
19	Carvalhas (Arganil)	Coimbra	29TNE7954	140	26-V-2015	x l	*P. spinosa*	PL	this study
20	Lousã	Coimbra	29TNE6436	670	4-VII-2015	x a		PL	this study
21	Torrozelas, Arganil	Coimbra	29TNE8551	515	16-VII-2015 5-VIII-2015 3-VI-2017 12-VI-2017 9-VII-2017 15-X-2017	x e x a x a x a x a xxx e	*P. spinosa* *P. spinosa*	PL	this study
22	Lamas D'Olo	Vila Real	29TPF0080 29TNF9980	980	26-VII-2015	x a		ALS	this study
23	Valbona, Arganil	Coimbra	29TNE8352	230	20-VIII-2015 29-VIII-2015 10-VI-2016 8-VII-2016 24-V-2017 30-VII-2017 1-VIII-2017 21-VIII-2017	x a x a x a x a x l x a + e x a + e x a	*P. spinosa* *P. spinosa* *P. spinosa*	PL	this study
24	Meixedo, Montalegre	Vila Real	29TPG0431	1000	02-VIII-2018	x a		AG	this study
25	Fraga da Pena, Arganil	Coimbra	29TNE9052	390	2-V-2017 15-X-2017	x l x e	*P. spinosa*	PL	this study
26	Seixo da Beira	Coimbra	29TNE9777	370	2-V-2017	x l	*P. spinosa*	PL	this study
27	Supegal, Miranda Corvo	Coimbra	29TNE5832	550	29-X-2018	x e	*P. insititia*	PP, SL	this study
28	Cabeça, Seia	Guarda	29TPE0763	500	1-XI-2018	x e	*P. insititia*	PP	this study
29	Loriga, Seia	Guarda	29TPE1264	860	1-XI-2018	xx e	*P. dulcis*	PP	this study
30	Sabugal	Guarda	29TPE6167	760	29-XII-2018	x e	*P. domestica*	PP, FR	this study
31	Fornos de Algodres	Guarda	29TPE2498	530	8-VIII-2021	x a		Carlos Mendes	this study

into Spain to the Sierra de Ayllón, east of Madrid), in the mountain ranges of Serra da Lousã, Serra do Açor, Serra da Estrela and Serra da Malcata. Northwards, we confirm the species' occurrence and expand it in the environs of Bragança (mountain ranges of Serra de Montesinho and Serra da Nogueira). A newly discovered but more fragmented cluster of populations is found from the northern border with Ourense (Galicia) near Boticas and Montalegre southwards to Serra do Alvão in the vicinities of the town of Vila Real. The species was also found through the observation of both adults and eggs in Serra da Peneda, but whether the latter populations are in contact needs confirmation. These recent and older observations make up about 31 known sites of occurrence of *T. betulae* in Portugal. A further handful of records from Serra da Malcata in Vicente Arranz et al. (2013b) could not be generally confirmed because of insufficient published data, with the exception of our own confirmation record near the town of Sabugal by the end of 2018. Our study thus provides an increase of about 428% in known Portuguese localities for *Thecla betulae*.

Known and projected distribution of *T. betulae*

Gathering all available information regarding *T. betulae* in the Iberian Peninsula, including published resources since García-Barros et al. (2004), references therein (Table 1), new records from Portugal (Table 2) and data mining of online databases such as GBIF, has allowed us to produce the updated distribution map in Fig. 1. The inclusion of online sources such as GBIF and iNaturalist has allowed for the inclusion of a further 16, 10 × 10 km UTM quadrats not covered by any other source of information.

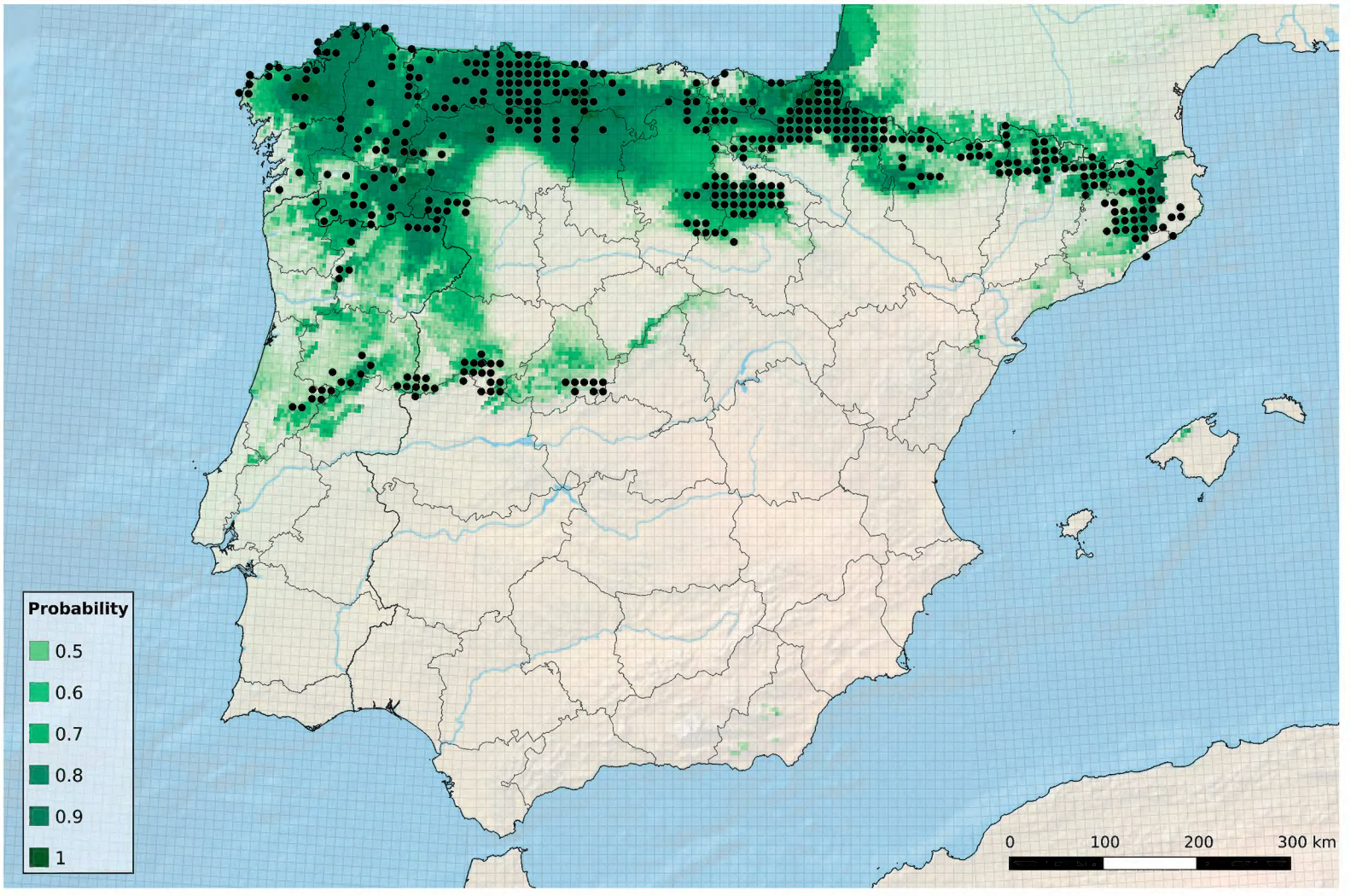

Figure 1. Updated Iberian distribution of *Thecla betulae* up to October 2021, including literature sources, online databases and fieldwork carried out during this study. In green, modelled distribution implemented in MaxEnt from 442 available presence points, under a resolution of 10km. Only a probability of occurrence above 50% is shown, darkest green shading representing areas with the highest probability of occurrence according to bioclimatic data.

From the map, it becomes clear that the actual Iberian distribution of *T. betulae* shows a mismatch from the one shown in most recent generalist European coverages of the species (Tchikolovets 2011; Leraut 2016), which do not extend its occurrence beyond the Pyrenees and the Cantabrian belt (but see Kudrna et al. 2015). In fact, the butterfly is found almost continuously from the pre-Pyrenean area and coastal ranges of Catalonia, in the east, through the Pyrenees, Cantabrian ranges as well as the temperate Eurosiberian areas north of these, westwards through to the Galician / Leonese ranges. As an offshoot, it colonises the temperate regions of the western Iberian Mountain System in Sierra de la Demanda and Sierra Cebollera (La Rioja, Burgos and Soria provinces) as well. In the extreme west, it is widespread in Galicia up to the coast and in northern Portugal, progressively higher up in mountain areas as going south to the Douro River near Vila Real.

As a (currently assessed) disjunct area of occurrence, *T. betulae* has been found in the Central Iberian ranges in several population pockets from Serra da Lousã to Serra da Estrela, in Serra da Malcata, Sierra de Gata to Candelario and in Sierra de Gredos. As yet, there are no records eastwards in the Sierra de Guadarrama or the Segovia province connecting the previously mentioned populations to the northern part of the distribution area via Spain.

The potential distribution model implemented in MaxEnt was built according to a defined set of bioclimatic variables encompassing abiotic constraints known to affect butterfly and other animal species (Fig. 1). It bears an AUC of 0.977±0.001, which is well above the 0.7 usually desired in such studies, meaning that the modelled species-distribution is very well explained by the used variables (Pearce and Ferrier 2000; Newbold et al. 2009). The projected distribution considers some currently under-sampled or poorly known areas as highly climatically suitable for the presence of *T. betulae*. Examples of such areas are the extreme North Aragon, the northern half of Burgos and Palencia provinces, most of Cantabria and westwards to the northern and western half of León following the more hilly and temperate landscapes. Western Zamora and the north-east of Trás os Montes in Portugal, all of Galicia but the lowlands of the south-west appear suitable too. The mountain ranges of all northern and central Portugal appear suitable too, possibly all the way southwards to the Gardunha range or even the Serra de Aire area. In the Central Mountain System of Spain, the species distribution could be connected from Sierra de Gata to Gredos and turns up as equally probable in the northern slopes of Sierra de Guadarrama, from where still no records are known.

Among the nineteen bioclimatic variables used, four were especially relevant for the model outcome. Hence, these four variables frame well the currently known distribution of *T. betulae* in Iberia. In decreasing order of importance these four variables are: bio 4 (Temperature seasonality), bio 9 (Mean temperature of driest quarter), bio 7 (Temperature annual range) and bio 12 (Annual precipitation) (Table 3). For a detailed explanation of all bioclimatic variables we refer to O'Donnell and Ignizio (2012). In short, *T. betulae* is positively affected by relatively stable temperatures over the year, particularly not too high during the summer and relatively high annual precipitation for the Iberian territory (Table 3). This translates into a temperate climate being essential for the presence of the species.

Ecology

There are some works dealing with the ecology and habitat resource preferences of *T. betulae* throughout Europe, much less is known from Iberia though.

In the whole of Eurasia, the species is known to select a number of shrub and tree species in the genus *Prunus* as hosts. It shows a preference for *P. spinosa* (sloe) but many other species have been recorded too, even in the allied genera *Crataegus* and *Chaenomeles*. Other recorded species are:

Table 3. Relative contribution of the bioclimatic variables used to build the *T. betulae* MaxEnt model of distribution. In each column the four highest values are highlighted. The % contribution measures the contribution of each variable to the regularised gain of the model, where the sum of each variable contribution must total 100. The permutation importance measures the drop in training AUC (in %) when permuting the values of each variable with the background values. Gain is a unitless statistic which assesses how well the predicted distribution fits the occurrence data compared to a uniform distribution. In 'Effect direction,' we translate the effect of the rise in values of given bioclimatic variable in the presence of the species: e.g. rising Bio 4 affects the presence of the species negatively.

Variable	Contribution (%)	Permutation Importance (%)	Gain	Effect direction
Bio4 Temperature seasonality	**28.6**	**30.8**	**1.22**	−
Bio9 Mean temperature driest quarter	3.1	**9.8**	**1.21**	−
Bio7 Annual temperature range	2.3	0	**1.19**	−
Bio12 Annual precipitation	0.7	**10**	**1.05**	+
Bio10 Mean temperature of warmest quarter	0.8	0.1		0
Bio17 Precipitation of driest quarter	**25.8**	4.6	0.9	+
Bio19 Precipitation of coldest quarter	**8.7**	0.9	0.9	−
Bio5 Max temperature of warmest month	0.5	4.6		+
Bio13 Precipitation of wettest month	0.7	1.7		+
Bio16 Precipitation of wettest quarter	0.7	0.9		−
Bio14 Precipitation of driest month	3.4	3.4	0.75	−
Bio18 Precipitation of warmest quarter	2.3	**13**	0.72	−
Bio11 Mean temperature of coldest quarter	0	0		0
Bio8 Mean temperature of wettest quarter	0.7	1		+
Bio2 Mean diurnal range	1.6	2.9		0
Bio1 Mean annual temperature	1.2	8.5		−
Bio15 Precipitation seasonality	4.5	6.9	0.5	0
Bio3 Isothermality	**13.9**	0.5	0.45	+
Bio6 Min temperature of coldest month	0.5	0.2		+

P. domestica, *P. insititia*, *P. avium*, *P. padus*, *P. persica*, *P. mahaleb*, *P. serotina*, *P. armeniaca*, *P. asiatica*, *P. mandchurica* and *P. cerasifera* (Dantchenko et al. 1995; Tolman and Lewington 1997; Tshikolovets 2011; Mortera 2015; Leraut 2016).

In Iberia, until very recently the only recorded food plant was *P. spinosa* but the burst of recent publications on the species has increased the number of known species. Iberian populations are now known to also include, in decreasing importance: 1) cultivated *P. domestica* or the wild and difficult-to-differentiate *P. insititia* (in Asturias, Catalonia, Extremadura and Castilla y León and in central Portugal); 2) *P. cerasifera* (Asturias); 3) *P. persica* (Catalonia); 4) *P. avium* (Extremadura) and *P. armeniaca* (Asturias). Other species have been repeatedly suggested as possible local sources, such as *P. mahaleb*, *P. padus* or *P. cerasus* but their use is still in need of confirmation.

Sequeira et al. (2011) list six native species of *Prunus* in Portugal: *P. avium*, *P. mahaleb*, *P. lusitanica*, *P. padus*, *P. spinosa* and *P. insititia.* Other species, such as almond (*P. dulcis*), peach (*P. persica*) and damascus (*P. armeniaca*) are widely present in orchards across the country. We retrieved the distribution of native species likely to be food plants in Portugal, according to Porto et al. (2021) (*P. spinosa*), Aguiar et al. 2021 (*P. insititia*) and Lourenço et al. (2021) (*P. avium*) and have represented their known distribution in Fig. 2. According to literature and our new records, the most recorded *T. betulae* food plants in Portugal are plum (*Prunus domestica*) and its wild relative *Prunus insititia*, and *P. spinosa. P. avium* and other less common host plants are yet to be confirmed in this territory, although one of the authors (PL) has witnessed egg-laying behaviour on

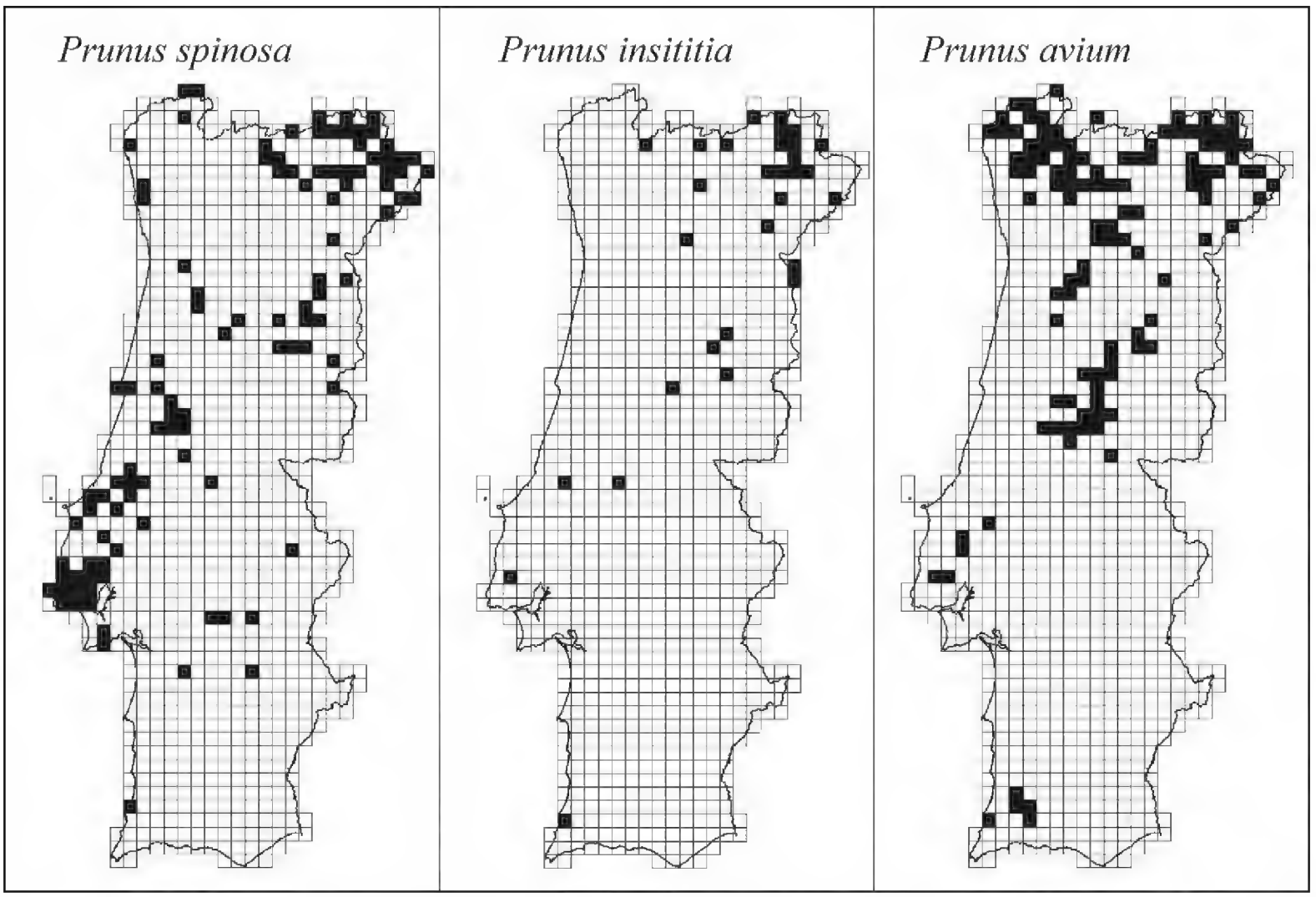

Figure 2. Distribution of potential native food plants in Portugal: *P. spinosa*, *P. insititia* and *P. avium* according to and adapted from Porto et al. (2021), Aguiar et al. (2021) and Lourenço et al. (2021), respectively.

Crataegus monogyna in Central Portugal. Furthermore, the butterfly has yet to be located in many areas where the potential food plants are more widespread such as Estremadura, Alentejo or most of Trás-os-Montes (Fig. 2). *P. spinosa* is particularly widespread in the limestone areas of central Portugal and in the north-east of the country but opportunistic searches for eggs of *T. betulae* in these areas have so far proven unsuccessful.

Positive results are mostly associated with hedges, old orchards and woodland margins under a temperate environment. Eggs were mainly found as singles in forks or near developing buds which would burst in spring time. However, clusters of up to nine eggs were found too (Fig. 3).

Whilst many potential areas with *P. spinosa* gave negative results for *T. betulae*, one of the most interesting outcomes of our field work was the detection of eggs on almond trees (*Prunus dulcis*). This *Prunus* species was hitherto unknown to be used by *T. betulae* (Fig. 3). The site where this observation comes from lies in the south-western part of Serra da Estrela, under a thermophilic situation allowing for the dozen 5–6 years old almond trees to grow, a condition not usually met in the remaining of *T. betulae* potential sites.

Life cycle

Iberian adult *T. betulae* records are scarce, as elsewhere, and most data derives from the observation of the early instars through direct search on the potential food plants. We now know that across Europe, females choose food plants with a certain profile: usually a fairly young or

Figure 3. *T. betulae* and its hosts in the field. **A.** Single egg on *P. domestica*, site 9, 1-XI-2009; **B.** Single egg on *P. dulcis*, site 20, 1-XI-2018; **C.** Same as previous; **D.** Same as previous. Arrow points to egg; **E.** Cluster of 8+1 eggs on *P. insititia*, site 12, 21-VIII-2014; **F.** L4 larva from site 1, reared from egg on *P. spinosa* collected IV-2008; **G.** One of the almond trees where eggs of *T. betulae* were located, site 20, 1-XI-2018.

younger-than-average branch of an isolated *Prunus* located on a sun-exposed forest-edge or hedge-row. It then descends to less than 2 m above ground where eggs are laid preferably singly in forks or near buds (Fartmann and Timmermann 2006; Merckx and Berwaerts 2010). In Iberia, the situation seems analogous but our own observations suggest a predominance of Portuguese records on older shrubs or even plum trees in perfectly established orchards, near villages where the eggs are often found in clusters of up to 9 (Fig. 3). However, these may be the result of several oviposition events, forced by the low availability of food plant resources in areas where the matrix is composed of *Eucalyptus* or *Pinus* agro-forestry.

Eggs or their remains may be found through the year but are the overwintering stage, from the end of the flight period until leaf burst in February or March. Upon hatching, young larvae eat the young leaves or flowers. The early-stages have been described in detail by Gómez de Aizpúrua (1991) and Muñoz Sariot (2011), while the larval ecology has been studied chiefly by Stefanescu (2000). Between feeding periods, the green dome-shaped larva rests on the underside of a leaf until mid-spring, reaching L3–L4 by the end of April in Catalonia (Stefanescu 2000). Caterpillars do not possess Newcomer's exocrine gland but the presence of perforated cupola organs (Malicky 1970) allow for them to be attended by at least two species of ants – *Formica rufibarbis* and *Lasius grandis* – in exchange for an amino acid solution reward (Stefanescu 2000; Muñoz Sariot 2011). Completion of the larval stage is reached by May or June and pupation happens among withered leaves on branches or down near the soil (Thomas and Emmet 1989; Muñoz Sariot 2011). Portuguese data agree with such cycle, with the greatest majority of eggs being found during Autumn and Winter, and larvae being found from February to May. The pupal stage has been found only once in July (Fig. 4 – dark shading).

In the rest of Europe, adults show an extended but univoltine flight-period from the end of June to October, varying with latitude and altitude, with a peak in August. Iberian data roughly agree, but observations from the Catalan Monitoring Scheme highlight a slight protandry with a male peak in early August and females extending their flight well into October when they are the only sex to be seen (Jubany and Stefanescu 2007). In the rest of Spain the very few records are centred in August to October. Portuguese adult observations, although representative of this general flight curve, seem to happen earlier than expected, from late May to September, peaking in August (Table 2, Fig. 4).

Butterfly behaviour is largely unknown because it takes place mostly at canopy level near the tree tops in light woodland. However, it seems that both sexes but particularly females do come down to soil level in the early morning to feed on nectar or dew-drops (Jubany and Stefanescu

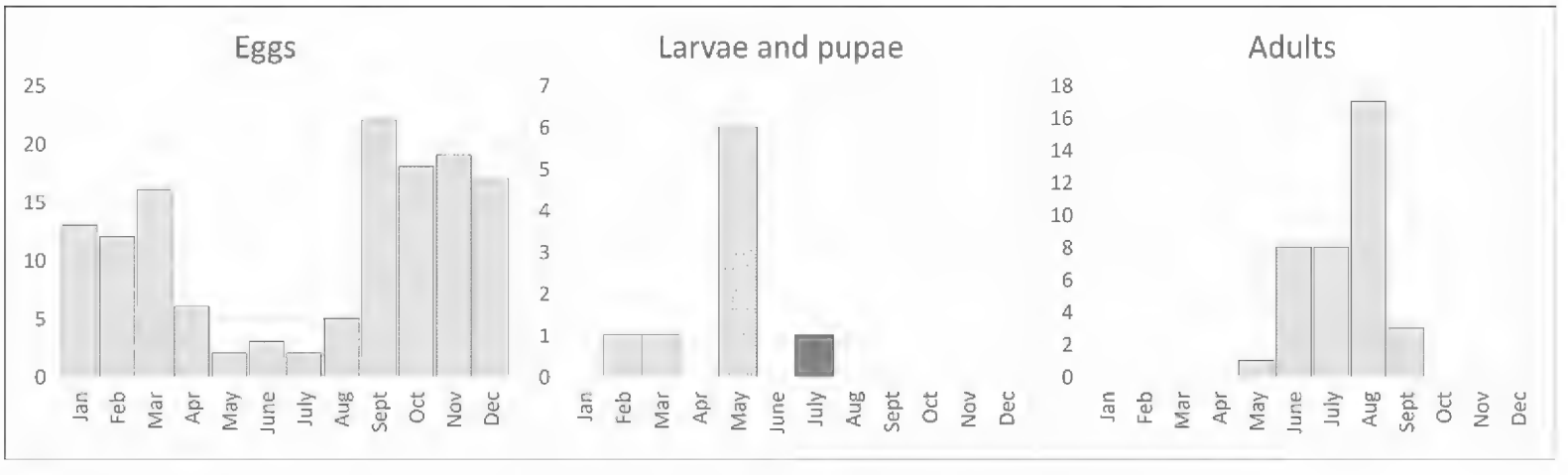

Figure 4. *T. betulae* life-cycle based upon Portuguese observations of the species.

2007). Later in the day, adult males congregate in particular trees, called 'master trees' (Thomas and Emmet 1989) which do not need to be food plants but are usually prominent features in the landscape. Here, they wait for passing females when courtship is initiated. In Iberia, this behaviour has been observed in Catalonia (Jubany and Stefanescu 2007) using *Sorbus aria* and *Quercus ilex* as master trees but is yet to be ascertained in the rest of the territory. According to the various references, the most observed behaviour of this butterfly is still oviposition by females at the end of the season, descending down the top branches backwards until about eye height to oviposit in rather secluded parts of the food plant. In Portugal, this type of behaviour accounts for many observations as well as just perching on sunlit portions of the canopy of the host plant (usually *Prunus spinosa*) or nearby shrubs and trees like *Quercus robur*, *Castanaea sativa*, *Salix atrocinerea* or *Betula pubescens*.

Discussion

Whilst *T. betulae* is an elusive species in the adult stage, the well-known and practised field-methods centred on the early stages have allowed for an above average amount of distribution and food plant data to be compiled. In the Iberian Peninsula, this has taken place increasingly in recent years following the Atlas of García-Barros et al. (2004), the publishing of a guide on the butterflies of Portugal (Maravalhas 2003) and the rise in the use of digital recording methods, social media and the subsequent sharing of information among experts and naturalists.

García-Barros et al. (2004) as the first work comprehensively mapping the presence of the species throughout Iberia likely promoted further studies with a more regional approach. Since this work, we have located about 17 other references dealing with the species in Iberian territory (Table 1), especially on the distribution and general biology topics. In Portugal, the late detection of the species in 1999 (Maravalhas 2003) delayed all possible assessments of the species until now. We believe the current study is the first one to present enough data so that it can be considered as a baseline knowledge of the species in the country, an assessment which may be extended to the whole of Iberia.

Because of all these new records since 2003, it felt necessary to properly update the knowledge about *T. betulae* in the south-western edge of its Palaearctic distribution area, the Iberian Peninsula. The aims of gathering new distribution data from fieldwork as well as data-mining from the literature allowed for the production of the up-to-date distribution map (Fig. 1). The map is a major improvement to the one previously available (García-Barros et al. 2004) and a clear depart from popular generalist European sources used by many throughout the continent (e.g. Tolman and Lewington 1997; Tshikolovets 2011, but see Kudrna et al. 2015). Based on these numerous sites, the resulting species distribution clearly indicates that it could well be present in many more areas, both in Portugal and Spain, particularly along the temperate forests and mountain areas connecting the known population pockets.

In fact, the species' modelled potential distribution according to bioclimatic variables confirms this hypothesis. Through this tool, we are able to identify where further search efforts should take place, in order to complete the Iberian distribution map of the species. Our study also identified the most likely bioclimatic factors that are driving the species' distribution in the Iberian Peninsula, at the boundary of its bioclimatic envelope and tolerance. In this respect, variables associated with a temperature and humidity stability throughout the year, seem to be strongly at play in constrain-

ing the distribution of the species in a peninsula with a predominantly Mediterranean climate. In fact, because the model converged so tightly with our newly available distribution data, its high confidence is a strong indicator that at least climatically, favourable areas still lacking research for *T. betulae* should harbour the species. We expect that this result will help in planning future fieldwork by naturalists and researchers in both Spain and Portugal.

Finally, this study also resulted in the discovery of almond (*Prunus dulcis*) as a new host-plant for the species in Portugal. It broadens the ecological spectrum of *T. betulae* towards a more Mediterranean environment. Furthermore, the discovery that the flight period of this species can start as early as late May in Portugal, in accordance with the often high temperatures that may be felt in some places, also supports this broadening of the niche, and highlights how novel life-history traits may still turn up in a relatively well known butterfly species.

Conversely, as more records and data of this species surface, its Portuguese demes seem to be at an increasing risk imposed by the spreading of *Eucalyptus globulus* monocultures and the invasion of semi-natural habitats by allocthonous trees in the genus *Acacia*, which is rampant in Central Portugal (Le Maitre et al. 2011; Martins et al. 2016). Adding to this ecological change through simple replacement of the flora comes the increasing fire-risk imposed by these aliens (Guerrero et al. 2021), which in 2017 and under particular weather conditions, culminated in massive wildfires which not only burnt a large part of Central Portugal (Comissão Técnica Independente et al. 2018) where these trees are now dominant, but also affected known areas for the occurrence of *Thecla betulae*, for example sites 17, 21 and 25. Following these forest fires, more aggressive management and fining measures were added to the countryside forested areas in Act 114/2017 29th December (updating Decree Law 124/2006), such as that land-owners are obliged to clear-cut vegetation 50 m around houses and along roads (Decree-Law 124/2006; Act 14/2017). Within such cleared land previously occupied by marginal vegetation elements such as *P. spinosa*, relegated there by monocultures, the available conditions cease to exist for the butterfly. Such imposes a conservation problem for *T. betulae*, a species already near its southern bioclimatic threshold of survival in Europe, which should be accounted for in any conservation status evaluation and investigated in the future.

Meanwhile, we believe that both the distribution data and the ecological framing of Iberian populations of this widespread Palaearctic species may certainly foster further studies and ultimately, a better comprehension of other elusive co-occurring species, that may be underrecorded as well.

Acknowledgements

We are truly indebted to the many recorders who contributed with their observations of eggs and adults of *T. betulae* in Portugal. These are listed in Table II. Without their records, support and local knowledge of the species the result would have been under par. We also thank Alejandro Lázaro Camafreita for interesting insights and suggestions regarding the species in Galicia and both him and José Rodrigo Dapena for the borrowing of relevant literature on the species. Furthermore, PP wishes to thank Paulo Tenreiro for showing his orchard full of *Prunus* in Brasfemes (Coimbra). Although no eggs were found in this orchard, it contributed to the growing interest in *T. betulae*. We further extend our acknowledgements to the two reviewers of an early version of the manuscript and the handling editor, all greatly improving this work.

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